A New Species of Ledermanniella (Podostemaceae) from Cameroon

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ABSTRACT. Ledermanniella prasina J. Schenk & D. W. Thomas in the family Podostemaceae, subgenus Ledermanniella, is proposed as a new species. It is known only from its type, collected at a single waterfall in Cameroon. The ecology, morphology, and variation among individuals are discussed. The new species is compared to the morphologically similar L. bifurcata, L. bowlingii, L. guineensis, L. jaegeri, L. minutissima, and L. monandra. Illustrations and a key to the monostaminate species in the subgenus are provided.

Key words: aquatic plants, Cameroon, Leder-manniella, narrow endemic, Podostemaceae.

With its center of diversity in Cameroon, Ledermanniella Engler is the second largest genus in Podostemaceae, consisting of about 44 species, which are all endemic to tropical Africa (Cook, 1996; Cusset, 1983, 1984). As defined by Cusset (1974), Ledermanniella is distinguished from other genera in the family through the combination of the following characters: the presence of alternate or whorled leaves, solitary or occasionally clustered flowers inverted within a closed spathellum, and an ovoid to ellipsoidal capsule with eight ribs. This broader classification ignored pollen and stamen number traits previously used and resulted in the inclusion of Inversodicraeia Engler and Monandriella Engler within Ledermanniella (Cusset, 1974). Subsequently, Cusset divided the genus into two subgenera, Phyllosoma and Ledermanniella, distinguished by the presence or absence of scalelike leaves, respectively (Cusset, 1983, 1984).

The new taxon is clearly a member of Podostemaceae due to its semi-aquatic habitat, thallus-like base (root), the presence of spathella, flowers that consist of two tepals, a syncarpous superior gynoecium with two styles, a single anther, and capsular fruit. The new taxon is placed in *Ledermanniella* based on its alternate leaves, solitary to clustered flowers each inverted within a closed spathellum, two filamentous tepals, flowers borne along shoots above a thalloid-root, and ellipsoidal capsules. It is placed in the subgenus *Ledermanniella* based on the absence of scale-like leaves and the presence of elongated leaves. The new species is known only from the type collection, which consists of approximately six pressed individuals along with 25 stems and shoots (which were separated from each other and/or other individuals at the time of collection), and two individuals along with 13 stems and shoots preserved in alcohol. Both collections have buds, flowers, and fruits in all stages of development.

TAXONOMY

Ledermanniella prasina J. Schenk & D. W. Thomas, sp. nov. TYPE: Cameroon. Southwest Province: 14 km NE of Mundemba, base of a large waterfall in the Mana River, between the villages of Miangwe 2 and Meta, 300 m, 5°02.4′N, 9°01.0′E, 01 Dec. 1998, Duncan Thomas 11550 (holotype, MO; isotypes, K, LBV, MO (preserved), NY, OSC, P, SCA, WAG, YA). Figure 1.

Speciebus monostaminiferis subgeneris *Ledermanniel-lae* similis sed distinguibilis seminibus smaragdinis et floribus (tepalis anthera gynoecioque includentibus) majoribus.

Semi-aquatic herbs from the spray-zone of a waterfall; thalloid-root disk-shaped, holdfast attaching plant to rock substratum; plants erect, 9–13 cm tall; main stem arising from thalloid-root, 1.0–32.0 mm long, 1.0–2.0 mm wide, erect; vegetative shoots arising from main stems, filiform, dichotomously branched, up to 7 cm long; fertile shoots arising from main stem, filiform, dichotomously branched, bearing reproductive structures; leaves up to 4 cm

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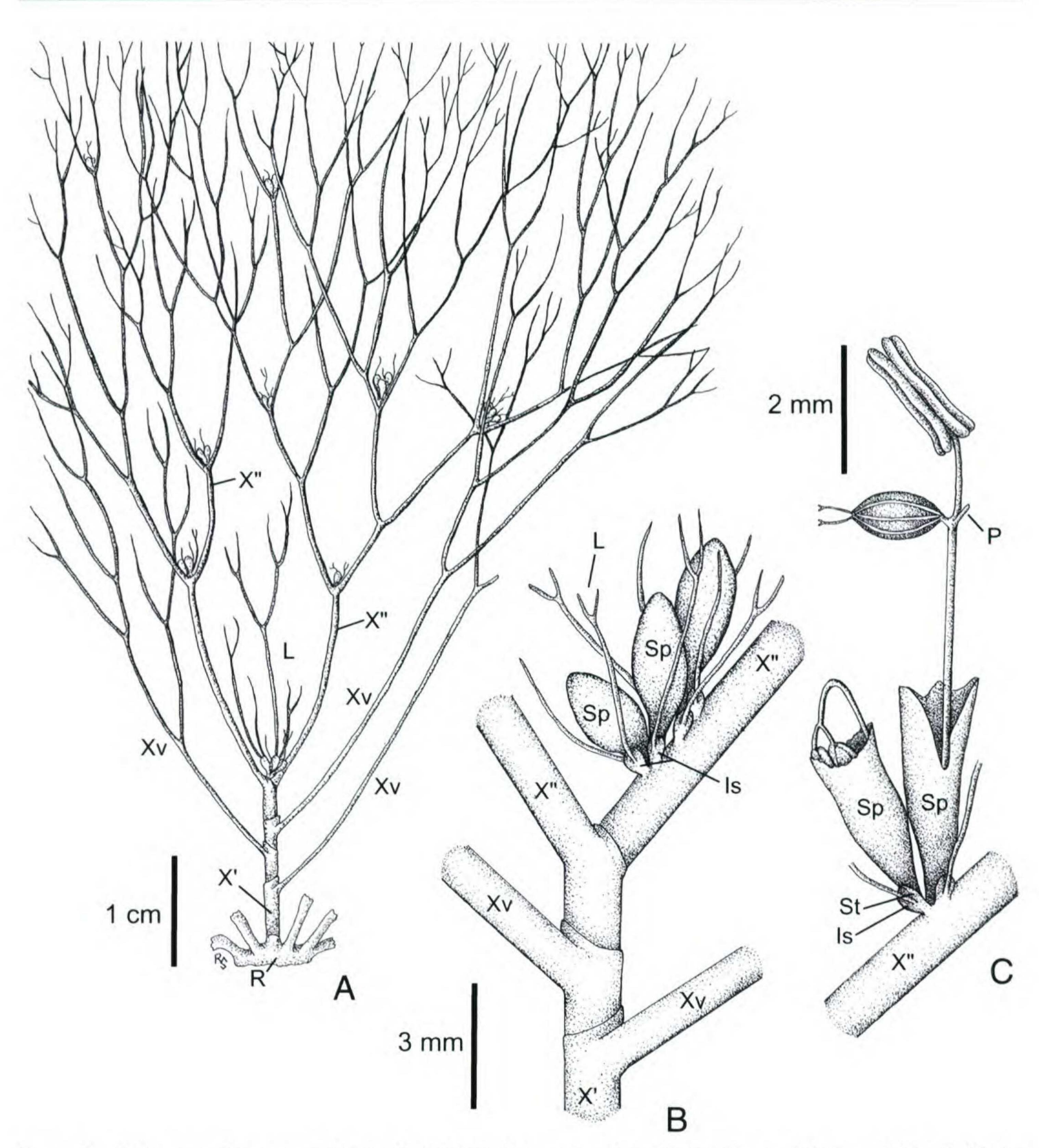


Figure 1. Ledermanniella prasina J. Schenk & D. W. Thomas, based on D. W. Thomas 11550. —A. Detailed habit of a single main stem showing the structure of the main stem (X'), fertile shoots (X"), vegetative shoots (Xv), leaves (L), and a thalloid-root (R; note that the apical portion and other mains stems are omitted for clarity). —B. A segment of the primary and fertile shoots showing the details of a flowering cluster, unruptured spathella (Sp) with leaves subtending spathella; also seen are stipules (St) located on the intrapetiolar scales (Is). —C. Ruptured spathella, with emerging, inverted flower (left) and fully emerged flower (right), along with tepals (P; only one of two shown).

long, 0.1–0.5 mm wide, dichotomously branched, solitary to verticillate below spathella, basal portion scale (intrapetiolar scale) with stipules, apical portion elongating from center of scale, filiform, glabrous; spathella erect, 3.0–8.0 mm long before dehiscence, 1.0–2.2 mm wide, ovate at beginning of development, then elongating to clavate, glabrous, solitary or in clusters (1–6) in the axils or along fertile shoots, apex globose to acute, dehiscence

mostly irregular, occasionally bilobed to trilobed; flowers solitary within spathella, zygomorphic, inverted prior to the opening of the spathella, upright after elongation, pedicel up to 13 mm long, tepals 2, acicular, 0.4–0.7 mm long, gynoecia 1.5(–1.7) mm long, 0.7–0.9 mm wide, attached to a gynophore, unilocular, styles 2, linear, 0.6–0.8 mm long, stigmas bilobed; stamens 1 (very rarely 2); filaments (= andropodium) 1.1–1.3 mm long at spa-

thellum dehiscence, 5.0–5.3 mm long after anthesis, alternate to the tepals; anthers basifixed, 2.0 mm long, 0.5–0.8 mm wide, longitudinally dehiscent; pollen white, in monads; capsules elliptic, 2.2–2.7(–3) mm long, 1.0–1.2 mm wide, bivalved, one valve persistent after dehiscence, the other caducous, ribs 8 per capsule, with 3 ribs per valve and 2 as the marginal sutures; placentas green; seeds bright emerald green, 0.3–0.4 mm long, 0.125–0.15 mm wide, ca. 25 to 37 per capsule.

ECOLOGY

Like many Podostemaceae, species of the genus Ledermanniella are sometimes narrowly endemic to a single geographical area (Cook, 1996). From our current knowledge, L. prasina occurs only at a single site, and is therefore narrowly endemic to the Mana River valley in the Rumpi Hills of Cameroon. On the basis of this information, it should be reddata listed as an endangered species according to the criteria established by the International Union for the Conservation of Nature (IUCN). The new species occupies a very unusual and specific habitat. The waterfall in the Mana River consists of two stages with a total height of approximately 100 m. At the bottom, there is a large, deep pool and a shelf of exposed gneiss bedrock, about 200 m² in extent; L. prasina occurs only on this shelf. The shelf is above the observed high-water level in the river, but its largely unvegetated state suggests periodic scouring, probably during occasional flash floods. The area has a very wet but strongly twoseasonal climate with a total annual rainfall exceeding 5000 mm. There is a short dry season December to March, with three months averaging less than 100 mm of rain. The first part of the wet season is typified by thunderstorms of varying frequency and duration, sometimes with dry periods of several weeks' duration. The wet season peaks in August and September, when monthly rainfall may exceed 1000 mm (Chuyong et al., 2004). This wet, seasonal climate, combined with the rugged, rocky topography of the Rumpi Hills, generates the type of river that is ideal for Podostemaceae, with a rocky bed and large seasonal variation in flow. With the exception of L. prasina, all Podostemaceae reported from Cameroon follow similar phenological patterns in response to this climate. The plants are obligate hydrophytes and grow submerged in fastflowing water during the wet season, attached to the rocks by thalloid-roots. When the water level in the rivers subsides at the beginning of the dry season, the exposed plants flower and fruit rapidly, after which at least the aerial parts die (Cusset, 1987;

Thomas, pers. obs.). Several species of Podoste-maceae exhibiting this phenology have been collected from the Mana River, including *Ledermanniella ledermannii* (Engler) C. Cusset, *Macropodiella pellucida* (Engler) C. Cusset, and *Saxicolella flabellata* (G. Taylor) C. Cusset (Cusset, 1987).

Ledermanniella prasina exhibits a very different habit and phenology, which is unique for the family in Cameroon. It does not grow submerged as most podostemads do, but instead has erect aerial stems and shoots that are kept moist throughout the growing period by spray generated from the waterfall. The spray is continuous during the wetter months with high water flow in the river, and it is this spray that supports the growth of the new species. The aerial shoots are intolerant of desiccation and wither rapidly when removed from the moist environment. In the dry season, the waterfall is present but much reduced in volume, and little spray reaches the rock shelf that supports the L. prasina population. During this period, the dry rocks appear to be largely devoid of vegetation and we do not yet know if L. prasina is annual, or if it passes the dry season as a dormant thalloid-root. Instead of having the short flowering period typical of Podostemaceae when the water level drops, the flowering and fruiting of L. prasina are prolonged and take place during the latter part of the growing season, when its fertile branches are produced. During this same period, the other Podostemaceae in the river are submerged and growing vegetatively, but they do not flower.

For several reasons, we do not believe that *Ledermanniella prasina* is a terrestrial form of one of the many other Podostemaceae that grow in the area. No other species of subgenus *Ledermanniella* have been collected from the Mana River. In addition, the *L. prasina* population is limited to a rock shelf, at least a meter above the high-water level, and does not extend down to the water, suggesting that it is intolerant of extended periods of submersion. Finally, some of the traits that separate the new species from similar species are structural or reproductive, and likely to be independent of habitat-related morphological plasticity.

MORPHOLOGY

Podostemads are difficult to describe in terms of standard angiosperm morphology due to their greatly reduced vegetative anatomy and unusual morphology. Distinguishing vegetative organs using cell and tissue orientation is an extremely difficult if not an impossible task (Rutishauser, 1995; Ameka et 230 Novon

al., 2003). The literature contains descriptive inconsistencies among the interpreted structures, demonstrating a general discordance of terminology and homology assessment among biologists studying Podostemaceae (Rutishauser, 1995; Sehgal et al., 2002). We use the terms "root," "main stems," "fertile shoots," "vegetative shoots," and "leaves" (Fig. 1) simply to describe this species; however, homology of such organs remains uncertain (Rutishauser, 1995, 1997).

The root structure is represented by an undefined thalloid tissue with a holdfast (= hapteron) located underneath. The function of the holdfast is to stabilize the plant by attaching it to the substrate. Botanists working with Podostemaceae use the term holdfast or hapteron, borrowed from algae terminology, to describe the superficially similar structure (Taylor, 1954; Hammond, 1937; Philbrick, 1984). The shape of the thalloid-root is described as being disk-like. However, the variability in thalloid-root shape is not fully understood in this species. The term "thalloid-root" is used to describe the undifferentiated tissue of which the main stem arises and that binds the plant to the substrate. There is no implication of homology to the familiar idea of a root since the structure has been suggested to be derived from a stem, a coalesced stem and root, or simply a modified root (Sehgal et al., 2002; Rutishauser, 1995). This term conforms to current literature and the root-shoot (CRS) model as the structure located underneath the main stem. However, much anatomical work needs to done on this plant as well as other podostemads before more concise determinations of homology can be made.

Approximately four to five main stems develop directly from the thalloid-root for each individual (Fig. 1A). The vegetative shoots and fertile shoots are borne on the main stem. The majority of the flowers are borne on the fertile shoots; however, some parts of the thalloid-root contain a shorter main stem of which there are no apparent vegetative or fertile shoots, but do have spathella subtended by leaves. It is not known if these stems elongate later in development and give rise to the vegetative and fertile shoots or remain as shorter dimorphic stems. This trait is not found in all individuals.

Two types of shoots are borne from the main stem, fertile shoots and vegetative shoots. The vegetative shoots branch dichotomously and appear leaf-like. There are two to three vegetative shoots borne on the main stem, before the fertile shoots arise (Fig. 1A). Located where the vegetative shoots diverge from the main stem, ligule-like structures are found that encircle it (Fig. 1A, B). The fertile shoots tend to be thicker than the vegetative shoots where they are borne on the main stem (Fig. 1A, B). They also differ by having reproductive structures along the branches and in the axils of dichotomous branches (Fig. 1A, B).

Leaves are located below the spathella (Fig. 1A–C). The basal portions of the leaves are scale-like, with an elongating thread-like leaf that dichotomously branches, similar in appearance to the vegetative stems. Stipules are located along the side of the scale. Ameka et al. (2003) referred to the basal scale as an intrapetiolar scale, which can also be rudimentary lateral stipules. We apply the term "leaves" to remain consistent with literature describing similar species (Ameka et al., 2003; Rutishauser, 1997; Hall, 1971; Taylor, 1954).

The spathella are quite variable in this species. The shape can vary from ovate to elliptic to clavate as they mature. It is also found that the spathella on the distal parts of the shoots are more ovate than those located toward the base. There is further variation in the spathellum margin following dehiscence. Most spathella have irregular margins following dehiscence; some, however, develop bilobed or trilobed margins.

The number of stamens is a variable character in this taxon as well as in other select species of Podostemaceae (Cusset, 1974). Two out of approximately 75 shoots have a single flower (each individual has approximately four to five shoots with an average of ca. 20 flowers per shoot) that contains two anthers attached to an andropodium (specimen housed at OSC). However, variability in anther number is rare enough that we continue to describe this species as monostaminate. Furthermore, a single individual was found containing two ovaries attached to a single gynophore (specimen housed at OSC). From our understanding of the group, this is a novel attribute for Ledermanniella. We could not find any literature documenting this mutation, suggesting its anomaly, and we therefore did not include it in the description.

The specific epithet "prasina" refers to the emerald green seeds that were removed from dehisced capsules. Less mature seeds seen inside undehisced capsules are also green.

Detailed comparisons were made between the new species and similar described species. The species selected for comparison included all monostaminate species from the subgenus, plus one species with two stamens. Published descriptions were used for the comparisons in all but two cases, where we needed to examine herbarium material.

Comparisons were made using herbarium material with the two monostaminate species, Leder-

manniella bowlingii (J. B. Hall) C. Cusset from Ghana and L. guineensis C. Cusset from Guinea. These two species were examined because they resemble the general habit of L. prasina: a single stamen, elongated shoots, intrapetiolar scale (L. bowlingii only), and linear leaf or leaf-like structures.

The herbarium material along with written descriptions demonstrate that Ledermanniella bowlingii differs qualitatively by having papillate spathella, pollen in dyads, inflorescence a cyme, and brown to reddish brown seeds, along with quantitative traits such as longer shoots, shorter tepals, smaller anthers, and smaller gynoecium (Hall, 1971; Cusset, 1984; Ameka et al., 2003). This was determined after examining the isotype (P) and a photograph of the holotype (K) along with descriptions and illustrations. Ledermanniella guineensis is distinguished from L. prasina by having a total length of one meter, inflorescence a cyme, a bilobed spathellum, the lack of leaves directly subtending the spathellum, smaller overall flower size, and brown to reddish brown seeds (Hall, 1971; Cusset, 1984). The holotype (P), along with four additional collections of Ledermanniella guineensis, was used for this comparison along with written descriptions and illustrations.

We did not use herbarium material to compare the three remaining monostaminate species Ledermanniella jaegeri C. Cusset, L. minutissima C. Cusset, both from Sierra Leone, and L. monandra C. Cusset from Cameroon, since the published descriptions of these species show they are very different. Both L. minutissima and L. jaegeri differ from L. prasina by containing leaves that subtend the spathella which lack intrapetiolar scales and dichotomous branching. Ledermanniella minutissima is further separated from L. prasina by possessing spathella that always arise from the thalloid or from a small shoot that is up to 3 mm long, and are always solitary (Cusset, 1984). Ledermanniella jaegeri has the additional character traits of leaves borne along the entire shoot instead of solely under the spathellum, as well as a more elliptic ovary (Cusset, 1984). Ledermanniella monandra appears to have an intrapetiolar scale; however, the leaves are borne on the entire length of the fertile shoot and are triangular in shape in contrast to the elongating leaves of L. prasina (Cusset, 1974, 1984).

The only bistaminate species investigated was Ledermanniella bifurcata (Engler) C. Cusset from Cameroon, Gabon, and Congo. Although it does have two stamens, it shares similar morphological traits, such as irregular spathella dehiscence, pollen in monads, and intrapetiolar scales, which are characters we felt needed further comparisons. Be-

sides the anther number, *L. bifurcata* differs by having an ovate spathellum (*L. prasina* also has an ovate spathellum, though it elongates to become clavate as it matures), a fertile shoot that widens at nodes (vs. no widening at nodes in *L. prasina*), leaves subtending the spathellum for the entire length of the shoot, shorter tepal length, smaller closed spathella, longer spathella pedicels, smaller anther size, and smaller gynoecium (Cusset, 1984, 1987; Hall, 1971).

KEY TO THE MONOSTAMINATE SPECIES OF LEDERMANNIELLA SUBG. LEDERMANNIELLA

- 1a. Leaves present under spathella, intrapetiolar scale absent, leaves do not branch dichotomously.

 - 2b. Shoots greater than 3 mm, leaves located along entire shoot L. jaegeri C. Cusset
- 1b. Leaves either absent under spathella, or if present, with dichotomous branching and intrapetiolar scale.

 - 3b. Leaves linear, greater than 2 mm long.
 - 4a. Spathella papillate, pollen in dyads L. bowlingii (J. B. Hall) C. Cusset
 - 4b. Spathella glabrous, pollen in monads.
 - 5a. Stems up to 1 m long, trailing in moving water; leaves absent below spathella; spathella arranged in a cyme; spathella bilobed at dehiscence; anthers 1 mm long; tepals 0.3–0.4 mm long; seeds brown/red L. guineensis C. Cusset
 - 5b. Plants 9–13 cm, erect on wet rock; leaves located below spathella; spathella solitary or in cluster; spathella irregular to bilobed at dehiscence; anthers 2 mm long; tepals 0.4–0.7 mm long; seeds emerald green L. prasina

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Literature Cited

Ameka, G. K., G. C. Clerk, E. Pfeifer & R. Rutishauser. 2003. Developmental morphology of *Ledermanniella*

- bowlingii (Podostemaceae) from Ghana. Pl. Syst. Evol. 237: 165–183.
- Chuyong, G. B., R. Condit, D. Kenfack, E. Losos, M. Sainge, N. C. Songwe & D. W. Thomas. 2004. Korup Forest Dynamics Plot, Cameroon. Chapter 29 in E. Losos & E. G. Leigh, Jr. (editors), Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network. Univ. Chicago Press, Chicago.
- Cook, C. D. K. 1996. The Aquatic Plant Book, 2nd Rev. Ed. SPB Academic Publishing, The Hague.
- Cusset, C. 1974. Contribution à l'étude des Podostemaceae: 4. Les genres *Ledermanniella*, *Monandriella* et *Inversodicraeia*. Adansonia, ser. 2, 14: 271–275.
- ——. 1984. Contribution à l'étude des Podostemaceae:
 8. Ledermanniella Engl. sous-genre Ledermanniella.
 Bull. Mus. Natl. Hist. Nat., B, Adansonia 3: 249–278.
 ——. 1987. Podostemaceae and Tristichaceae. Pp. 51–

99 in B. Satabié & P. H. Morat (editors), Flore du Came-

- roun Vol. 30. Ministère de l'Enseignement Supérieur et de la Récherche Scientifique, Yaoundé.
- Hall, J. B. 1971. New Podostemaceae from Ghana with notes on related species. Kew Bull. 26: 125-136.
- Hammond, B. L. 1937. Development of *Podostemum ceratophyllum*. Bull. Torr. Bot. Club 64: 17–36.
- Philbrick, C. T. 1984. Aspects of floral biology, breeding system, and seed and seedling biology in *Podostemum* ceratophyllum (Podostemaceae). Syst. Bot. 9: 166–174.
- Rutishauser, R. 1995. Developmental patterns of leaves in Podostemaceae compared with more typical flowering plants: Saltational evolution and fuzzy morphology. Canad. J. Bot. 73: 1305–1317.
- Sehgal, A., M. Sethi & H. Y. Mohan Ram. 2002. Origin, structure, and interpretation of the thallus in *Hydrob-ryopsis sessilis* (Podostemaceae). Int. J. Pl. Sci. 163: 891–905.
- Taylor, G. 1954. Podostemaceae. Pp. 122–127 in J. Hutchinson & J. M. Dalziel (editors), Flora of West Tropical Africa, vol. 1, 2nd ed., revised by R. W. J. Keay. Crown Agents, London.